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THE TAXONOMIC STATUS OF *HEPTAXODON* AND DENTAL ONTOGENY IN *ELASMODONTOMYS* AND *AMBLYRHIZA* (RODENTIA: CAVIOMORPHA)

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No. 5 — *The Taxonomic Status of* Heptaxodon *and Dental Ontogeny in* Elasmodontomys *and* Amblyrhiza
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INTRODUCTION

The affinities of the extinct Puerto Rican caviomorph, *Heptaxodon bidens* Anthony 1917, have been problematical owing to the supposed reduction of cheek teeth to two on either side above and below, with the first strongly dominant. This condition, grossly aberrant for a caviomorph, led some authors to isolate *Heptaxodon* in its own monotypic family (Miller and Gidley, 1918, p. 447, followed by Anthony, 1926, p. 130) or subfamily (Anthony, 1917, p. 186; 1918, p. 397). Others have included it in a subfamily (Simpson, 1945, p. 96, followed by Wood, 1955, p. 182) or family (Landry, 1957, p. 59) together with five[2] other West Indian genera. If the stated diagnostic characters of *Heptaxodon* are accepted at face value, association at the familial level with any known genus of caviomorph seems indefensible. The down-grading in taxonomic isolation of *Heptaxodon* in the more recent works cited above undoubtedly reflects a growing disbelief in the reality of its apparent uniqueness, but it was H. G. Stehlin (*in* Stehlin and Schaub, 1951, p. 262, followed by Schaub, 1958, p. 736) who first interpreted the genus as a growth stage of *Elasmodontomys obliquus* Anthony 1916. This author arrived at the correct conclusion on the invalid premise that the dominant cheek teeth of *Heptaxodon* are $P\frac{4}{4}$ of *Elasmodontomys*. X-ray photographs of critical specimens, restudy of all dentigerous elements of *Heptaxodon*, *Elasmodontomys*, and *Amblyrhiza* in the collections of the American Museum of Natural History (AMNH) and the Museum of Comparative Zoology (MCZ), and comparisons with developmental patterns in hystricomorphs and in other caviomorphs have shown, as pointed out in detail below, that the anterior cheek teeth of *Heptaxodon* are $DP\frac{4}{4}$ of *Elasmodontomys*. This review of the evidence has made possible a better understanding of dental ontogeny in *Elasmodontomys* and *Amblyrhiza*.

[1] This work was completed while the author was Assistant Curator in charge of fossil vertebrates at the Florida State Museum, University of Florida, Gainesville.

[2] Six, if *Quemisia*, omitted by the above authors, were included in the group, as it has been to the present by all authors who have discussed it.

A word is necessary here regarding nomenclature of tooth components. Stirton (1935, p. 392) has derived from the tritubercular system a terminology for beaver teeth, and Fields (1957, p. 278) has extended it with additions to certain late Miocene dinomyids, pointing out that ''the application of these terms does not necessarily imply homology but has been used as a matter of convenience.'' I have not felt justified in extending to the highly evolved, hypsodont *Elasmodontomys* a system which ordinarily carries some connotation of homology. Further, the structure of the *Elasmodontomys* cheek tooth is so elegantly simple that it is most conveniently described in neutral geometric and numerical terms.

Cope (1883, p. 5) has aptly characterized the units of which the cheek tooth of *Amblyrhiza* is composed as ''columns of dentine inclosed in . . . a sheath of enamel,'' a description equally appropriate for *Elasmodontomys*. The columns and their sheaths are flattened anteroposteriorly and closely applied to one another, with a small amount of cementum interspersed. Successive columns are separated by transverse reëntrants that penetrate the full width of the tooth. Each reëntrant may be designated as outer or inner depending on whether its deepest proximal extension is labial or lingual. Individual columns and reëntrants may be distinguished by numbering them serially from anterior to posterior in each tooth. The enamel of the anterior wall of each column (and thus the posterior wall of each reëntrant) is much thicker than that of the posterior wall (anterior wall of reëntrant) in the upper teeth, and vice versa in the lower teeth. In both upper and lower teeth the free external enamel walls are invariably thick. Much confusion has arisen in describing these teeth as a result of inconsistent reference to either columns or reëntrants, and as a result of failure to detect the thin enamel walls, which appear only as hairlines on occlusal surfaces. The occlusal pattern of each column obliquely sectioned by wear takes the form of a much flattened ellipse. In some cases, even in long, little-worn teeth some reëntrants are not completely penetrant but have their vertex tightly appressed to the adjacent external enamel wall so that it is visible far down the shaft of the tooth through the translucent external wall. In such cases, and in senescent teeth in which the enamel forms a single continuous trace on the occlusal surface, the pattern produced by each column is more appropriately designated a loop.

Development of the lower dentition of *Elasmodontomys* will be treated first, followed by the less well documented upper dentition of *Elasmodontomys*, and that in turn by the fragmentary data on *Amblyrhiza*. Length of a given tooth is in all cases a maximum taken parallel to the longitudinal axis of the tooth, including roots where present. Selection of genera for comparison has been in part dictated by the availability of appropriate ontogenetic stages, and no *a priori* implication of relationship is intended.

I wish to thank Professor Bryan Patterson, who initiated the present study, for generously turning over to me X-rays prepared by Dr. Rainer Zangerl of the Chicago Natural History Museum (CNHM) together with the drawings by Mrs. Dorothy Marsh that are reproduced in Figures 1 and 2. I wish to thank also the curators in the Department of Vertebrate Paleontology, American Museum of Natural History (AMNH), who permitted free use of the splendid collection of Antillean caviomorphs accumulated largely by H. E. Anthony; and the curatorial staffs of the mammal departments of the American Museum of Natural History, Chicago Natural History Museum, and Museum of Comparative Zoology (MCZ) for making available modern comparative material.

DENTAL ONTOGENY

Lower Dentition of *Elasmodontomys*

Certain critical specimens are described below in detail in order of increasing age, followed by a discussion of development and comparisons with other genera. AMNH 55030 and 55031, and MCZ 10132 have always been regarded as "*Heptaxodon*," whereas AMNH 55037, in spite of its DP_4, was identified quite correctly as *Elasmodontomys*.

AMNH 55030. Left ramus with DP_4 (Fig. 1A). Figured by Anthony (1917, pl. 5, figs. 4, 6; 1918, fig. 38C, D, F; 1926, fig. 48C, D, F). Mandibular symphysis open. Bone porous in texture. DP_4 with five columns, the first with a small, semi-isolated subsidiary pillar on its anterolingual wall, the pillar unworn, merging with the column at the alveolar border; the fourth column with a constriction in the middle of its occlusal surface. Occlusal area small; obviously it would have increased with additional wear. The X-ray photograph shows incipient double roots of DP_4 (reflected externally by a bulge on the ventral
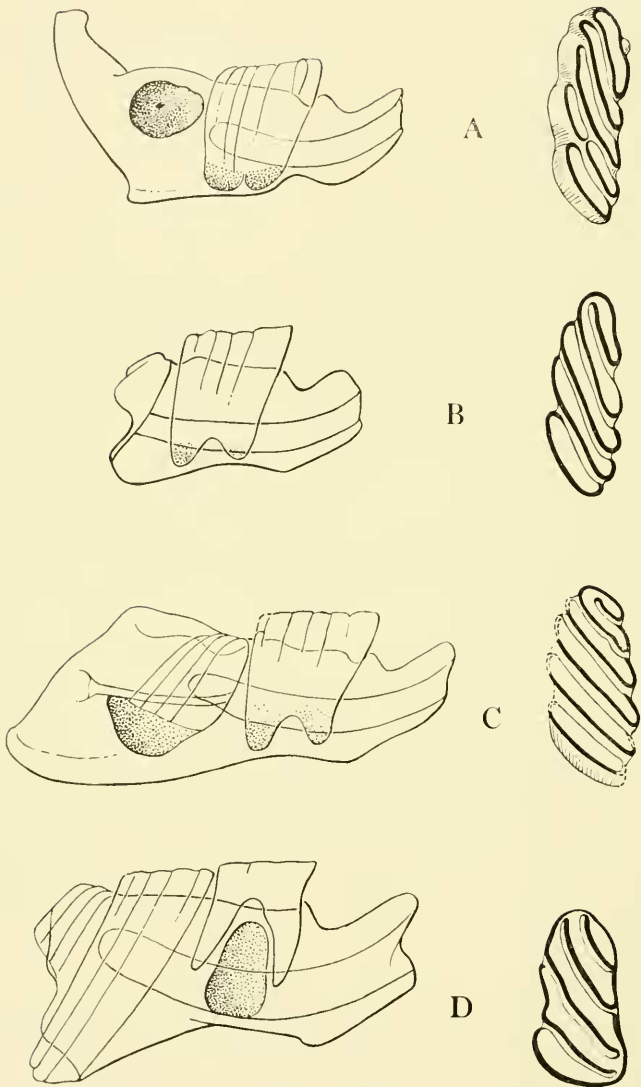
FIGURE 1. Early ontogeny of the lower dentition in *Elasmodontomys obliquus*, showing on the left (approximately × 1.1) immature left mandibular rami in lingual aspect, diagrammatically represented largely on the basis of X-ray photographs, and on the right (approximatey × 2.2) the corresponding DP_4 in occlusal aspect. In order of increasing age the specimens figured are: *A*, AMNH 55030; *B*, AMNH 55031; *C*, MCZ 10132; *D*, AMNH 55037.

border of the horizontal ramus), the crypt for M_1 (the thin walls of which are broken through in three places), and the base of the incisive alveolus adjacent to the posterior border of DP_4. Length of DP_4 approximately 16 mm.

AMNH 55031. Left ramus with DP_4 and M_1 (Fig. 1B). Symphysis open. Bone porous. DP_4 with five columns, the first two confluent anterolabially, the last two merging lingually 2.6 mm proximal to occlusal surface. Occlusal surface near its maximum area. M_1 apparently just at point of eruption; its columns open proximally. Incisive alveolus terminating adjacent to middle of M_1. X-ray photograph shows DP_4 with well formed double roots. Length of DP_4 slightly less than 15.8 mm.

MCZ 10132. Left ramus with DP_4 and M_1 (Fig. 1C). Age apparently comparable to AMNH 55031. Symphysis open. Bone porous. DP_4 with six columns, the first of which is subsidiary and confluent anterolabially with the second, with which it merges lingually 3.5 mm proximal to occlusal surface. Length of DP_4 less than 17 mm. Discovery that DP_4 was loose in its alveolus made possible direct confirmation of the interpretation of the X-ray photographs which indicated well-formed double roots, and in addition revealed that the posterior root is subdivided transversely into two rootlets. M_1 is just at the point of eruption but quite unworn, revealing minor subdivisions near the apices of its unworn columns which would have been expressed ephemerally at early stages of wear as isolated islands and as constrictions in the characteristic ellipses. There are four major columns with a fifth, anterior, minor one confluent anterolabially with the first major one. Incisive alveolus terminating adjacent to middle of M_1.

AMNH 55037. Left ramus with DP_4, M_1, and M_2 (Fig. 1D). Symphysis open. DP_4 deeply worn, with all five enamel columns confluent and the trace of the enamel a complex but continuous line on the occlusal surface. The occlusal area is much reduced. The tooth apparently has slipped partially out of its alveolus and subsequently become cemented in that position, revealing the bases of two strongly developed roots with the saddle between them only 4.8 mm below the occlusal surface. Including the long roots, the tooth is no less than 13 mm long. A small hole inside the alveolus between the roots of DP_4 opens into a large crypt for P_4. No trace of P_4 itself was detected. M_1 is in full use, its enamel sheaths confluent at their exposed proximal ends indicating termination of enamel growth; no trace of root formation. Length of M_1 is 32.1 mm. Longitudinal axis

of M_1 widely divergent from crypt of P_4, directed posteroventrad at angle of about 60° to occlusal surface, extending into angular process to the ventral border. M_2 at point of eruption, unworn, consisting of four columns open at their bases, maximum length 15.6 mm. Incisive alveolus terminating adjacent to posterior margin of M_1.

AMNH 55041. Left ramus with M_2 and alveoli of P_4 and M_1. Symphysis tightly fused dorsally but open ventrally. P_4 alveolus very deep, producing prominent bulge on ventral border of jaw. The alveolus has a small concavity on its anterior wall near the alveolar border, which may be the vestige of the alveolus of the anterior root of DP_4, suggesting shedding of DP_4 only slightly prior to the stage here represented. M_2 is in full use, its columns confluent proximally indicating cessation of their growth. The tooth slopes posteroventrad so that its occlusal surface is highly oblique to its longitudinal axis. The base of the tooth lies posteroventral to the mandibular foramen. There is no external indication of M_3, but there is sufficient space that the crypt and tooth primordium could be accommodated. The specimen has not been X-rayed. Incisive alveolus terminates adjacent to middle of M_2.

AMNH 17137 h. Right ramus with P_4-M_3. Figured by Miller (1929, pl. 4, fig. 1, 1a). P_4-M_2 in full use, whereas M_3 is not erupted. Incisive alveolus terminating adjacent to middle of M_2.

The growing tip of the lower incisor of *Elasmodontomys* extends with increasing age progressively posterad, as far as the middle of M_3 in the oldest observed jaw (AMNH 55039). A similar sequence occurs in *Dinomys*. In the youngest observed individual (AMNH 100011, M_2 in initial wear) the tip lies at the posterior edge of M_2; in AMNH 100053 (M_3 erupting), at the posterior edge of M_3; in AMNH 46551 (DP_4 much worn), well behind M_3. No such progression occurs in *Dasyprocta*; in individuals with only DP_4 in use the growing tip of the incisor already extends posteriorly almost to the mandibular foramen.

Anthony (1918, p. 399) considered that, "the [pre-] molar of *Heptaxodon* is a logical development from a tooth like that of *Elasmodontomys* in which genus a tendency toward multiplication of the laminae of the individual tooth has been noted, this increase in number of plates being accompanied by an apparent decrease in the number of the teeth." These differences

are here shown to be ontogenetic rather than phylogenetic. The differences in number of columns and in the related shape of occlusal surface between DP_4 (*"Heptaxodon"*) and P_4 in *Elasmodontomys* are analogous to those between the same two teeth in *Dasyprocta*, *Cuniculus*, and *Dinomys*. The "*Heptaxodon* molar" (DP_4) has five (six in MCZ 10132) enamel loops on its triturating surface as compared to four loops in P_4 of *Elasmodontomys*. In correlation with its greater number of enamel ellipses the occlusal surface of DP_4 is anteroposteriorly elongate whereas in P_4 of *Elasmodontomys* it is trigonal and more nearly equidimensional. DP_4 of *Dasyprocta* has six transverse enamel units (each composed of two laminae of enamel with the intervening dentine) and is conspicuously elongate anteroposteriorly, whereas P_4 has five transverse units and is subequidimensional. DP_4 of *Cuniculus* has an anteroposteriorly elongate crown with at least four lingual reëntrants, the most anterior of which is complex, whereas P_4 has three simple lingual reëntrants, and an equidimensional crown. In *Dasyprocta* and *Cuniculus* the enamel does not form well-defined ellipses on the triturating surface as it does in *Elasmodontomys* and in *Dinomys*. DP_4 of *Dinomys* is composed of four discrete columns of enamel, as compared to three columns in P_4 (an unworn P_4 in AMNH 46551 has a small cylindrical fourth column on its anterior face which merges proximally with the adjacent column).

As might be expected, the number and configuration of the enamel ellipses or loops in DP_4 of *Elasmodontomys* (and in *Dasyprocta*, *Cuniculus*, and *Dinomys*) varies individually and with degree of wear. In AMNH 55030 (Fig. 1A) DP_4 is in the initial stages of wear, as indicated by the small area of the wear surface and by the division of the next to last enamel ellipse into two ellipses. The tooth is peculiar in the presence of a subsidiary pillar of enamel on its anterior face. The pillar is unworn but would be expressed on the wear surface by a small circle of enamel. With additional wear the area of the triturating surface would undoubtedly increase, the two ellipses unite, and the small pillar disappear, producing a crown pattern not unlike that of AMNH 55031. The condition of DP_4 in extreme wear is illustrated by AMNH 55037 in which the enamel no longer forms complete ellipses but forms one continuous trace on the wear surface. MCZ 10132 and AMNH 55031 are of approximately the same age, judging by similar gross

size, wear of DP_4, development of M_1, and length of incisor alveolus. However, DP_4 has six enamel loops in MCZ 10132 and only five in the other three jaws. This additional loop can be ascribed to individual variation (perhaps as an expression of the same genetic tendency producing the small pillar in AMNH 55030) and undoubtedly would disappear with additional wear. Stehlin and Schaub (1951) referred to the "*Heptaxodon* molar" as a "frischer Prämolar," implying that the added enamel ellipses and elongate occlusal surface would be transformed by wear and (everlasting) growth into the configuration expected in P_4 of *Elasmodontomys*. That no such trend occurs is well shown by Figure 1D, demonstrating conclusively that the tooth in question is long-rooted and very nearly worn out before M_2 is erupted. The double-rooted, moderately hypsodont first molariform tooth in each jaw shown in Figure 1 is quite in contrast to the single-rooted extremely hypsodont permanent molariform teeth of *Elasmodontomys* (such as M_1 in Fig. 1D), indicating that the first tooth is deciduous. The permanent molariform teeth of *Elasmodontomys* differ from those of *Dinomys* in that they are not evergrowing, a fact which was recognized by Anthony (1918, p. 383). Anthony, nevertheless, considered the molariform teeth of *Elasmodontomys* to be rootless, although he accurately described and illustrated the deposition of cement beyond the base of the enameled portion of the teeth. To me this deposition seems to be acceptable as root formation. In none of the isolated teeth available is the root entirely closed, but none of these teeth is in an advanced stage of wear. In a fragmentary left ramus (AMNH "4") the root of a deeply worn M_1 is visible and broken in transverse section. The root is quite solid with the exception of a fine central canal. In the oldest available ramus (AMNH 55039), P_4. M_1, and M_2 are worn almost to the base of the enamel with long roots broadly exposed. M_3 is absent, but its well-preserved, conical alveolus tapers to a sharp apex clearly indicative of a closed root. The order of termination of enamel growth (and presumably also of root growth) of the molariform teeth is DP_4. M_1, M_2, P_4, M_3. That DP_4 terminates its growth first is self-evident and as expected. In AMNH 55037 (Fig. 1D), M_1 has terminated its enamel growth prior to the formation of P_4 and during the early growth of M_2. The conclusion that growth of M_2 terminates before that of P_4 is based on the advanced growth of M_2 in AMNH 55037, in which P_4 remains to be formed. The

bases of all four molariform teeth are exposed in AMNH 55044 revealing that P_4, M_1, and M_2 have well-formed open roots whereas M_3 has terminated its enamel growth but formed no root. The termination of enamel growth in a given tooth seems to coincide with the initial wear of that tooth. This coincidence has been observed for DP_4 (AMNH 55030, Fig. 1A), M_1 (AMNH 55037, Fig. 1D), and M_3 (AMNH 55044). The appropriate stages for the demonstration of this feature in P_4 and M_2 are not available.

In *Elasmodontomys*, P_4 comes into use prior to M_3, as shown by AMNH 17137j in which P_4 is considerably worn and M_3 is unerupted. Anthony apparently considered this to be the established sequence in all hystricomorphs (including caviomorphs) for he concluded that the functional tooth in *"Heptaxodon"* was a fourth premolar on the basis of "the great importance in the hystricomorph tooth row assumed by the last premolar, since it always becomes functional before the last molar. . . ." (1918, p. 398). However, M_3 (and M^3) becomes functional prior to P_4 (and P^4) in *Hystrix, Atherurus, Erethizon, Dinomys, Olenopsis* (Fields, 1957, p. 327), *Dasyprocta*, and *Cuniculus*,[2] and the $P\frac{4}{4}$ are entirely suppressed in modern echimyids and capromyids and thus of course do not precede the $M\frac{3}{3}$ (Wood and Patterson, 1959, p. 301).

The overall sequence of eruption in *Elasmodontomys* is DP_4, M_1, M_2, P_4, M_3, identical to the sequence of termination of enamel growth, as might be expected. DP_4 is shed after the eruption of M_2, as shown by AMNH 55037 (Fig. 1D), and (obviously) prior to the eruption of P_4 (or technically shortly afterwards, for DP_4 may have remained functional after P_4 had thrust up between its roots, above the alveolar border, as noted below in *Dinomys*).

Tooth formation in *Elasmodontomys* apparently was very rapid. In AMNH 55030, for example, there is no trace of M_1 other than its crypt, whereas in AMNH 55031 and MCZ 10132 M_1 is well formed and on the point of eruption. The amount of wear incurred by DP_4 during this interval is only moderate.

[2]Individuals of appropriate age were fewer than desirable for all forms mentioned, but only in borderline cases would variation be expected to be so great as to affect sequence. One such borderline case was noted in caviids in which a specimen of *Microcavia australis* (MCZ 18995) was observed with $DP\frac{4}{4}$ and $M\frac{3}{3}$ in use, whereas a specimen of *Cavia porcellus* (MCZ 9426) and one of *C. tschudii* (MCZ 17736) have $P\frac{4}{4}$ in full use and $M\frac{3}{3}$ barely breached by initial wear.

Similarly, DP_4 in AMNH 55037 is worn almost to the base of its enamel, but P_4 remains unformed although its crypt is present. In a specimen of *Dinomys* (AMNH 46551) the left DP_4 has been broken off revealing a large P_4, the crown of which stands well above the alveolar border. The right DP_4 of the same individual is in place and much less worn than the same tooth in AMNH 55037.

The straight-line distance between the tip of the angular process and the anterior extremity of the jaw in MCZ 10132 (the only "*Heptaxodon*" jaw on which any sort of length measurement could be taken) is 54.5 mm, or about 60 per cent of the similar measurement in an adult jaw of *Elasmodontomys* (90.0 mm in AMNH "4"). In *Dasyprocta* the corresponding figures are 36.9 mm in MCZ 28091 (developmental stage comparable to MCZ 10132) and 60.0 mm for MCZ 32012, a young adult, again giving a percentage slightly greater than 60. Undoubtedly the precise correlation between these growth stages in *Dasyprocta* and *Elasmodontomys* is fortuitous, but it does indicate that the increase in gross size demanded of "*Heptaxodon*" in order for it to develop into *Elasmodontomys* is not unreasonable.

Upper Dentition of *Elasmodontomys*

Anthony concluded that AMNH 17101 should represent the type of a new genus with remarkably reduced dentition on the basis of the following premises:

1. The type palate "bears all the appearance of maturity" (1918, p. 398).

2. "The second and last tooth . . . appears to be an unworn tooth, not yet above the gum, but . . . may well be regarded as having dropped deeper into the alveolus than the normal position" (1917, p. 184).

3. "It is apparent from the fragment [of the palate] that there is room for no more than the two teeth" (1917, p. 184).

If the first observation is correct then the third furnishes valid evidence for the conclusion that the molariform teeth are reduced to two in each series, but if the palate (and the lower jaws) is that of a juvenile individual, it would not be expected to accommodate the full adult dentition. Anthony apparently did not consider the possibility that the palate (and the lower jaws) might be young enough for the functional tooth in each series to be a deciduous premolar. Although the bone of the palate is rather dense in texture, the fact that M^1 is little developed (maximum possible length 10.9 mm compared to

25-30 mm for M^1 with crown complete, but lacking root) and unerupted, and that the palatal sutures are open, clearly indicates that the specimen is immature. There is no indication that M^1 has "dropped deeper into the alveolus than the normal position." Assuredly it was not yet a functioning tooth, but was on the verge of eruption. The developmental stage of AMNH 17101, the type palate, approximates most closely that of MCZ 10132 among the lower jaws.

An ontogenetic sequence similar to that proposed here from "*Heptaxodon*" to *Elasmodontomys* occurs in *Dasyprocta*. Several young individuals of *Dasyprocta* (MCZ 28091, 34962, 34963) were observed to have in use only the well-worn deciduous fourth premolars with the first molars just at the point of eruption. This condition is comparable to that in AMNH 55031 (Fig. 1B) and MCZ 10132 (Fig. 1C). Obviously there is a considerable period in the early growth of *Dasyprocta* during which the deciduous fourth premolars constitute the entire cheek tooth battery, as in "*Heptaxodon*." In spite of this, the adults have the more orthodox formula of one premolar and three molars in each series, as in *Elasmodontomys*. DP^4 of *Elasmodontomys* is composed of seven columns of enamel, the first two of which merge labially less than one mm proximal to the occlusal surface, and the last two of which are confluent lingually at the occlusal plane and merge labially as well about two mm proximal to it. Just as in the lower dentition, DP^4 in *Dasyprocta, Cuniculus, Dinomys,* and *Elasmodontomys* has a longer occlusal surface made up of more units than does P^4. In the upper dentition of *Elasmodontomys*, both DP^4 (with seven) and P^4 (with five) have more enamel columns than their inferior counterparts (DP_4 with five or six, P_4 with four).

Unfortunately, documentation for dental succession is less satisfactory for the upper dentition than for the lower. However, it is clear from AMNH 17101 that DP^4 only is in use for a considerable period in early ontogeny, and that it is followed in eruption by M^1. The next stage represented is that of AMNH 17132 with P^4-M^2 in use on either side and without trace of M^3 or space for its development. Anthony (1926, pp. 108-109) tentatively interpreted this specimen as an example of evolution by discontinuous variation, supposing that the molars were reduced to two, and that the occlusal length of P^4-M^2 was increased to compensate the suppression of M^3. In fact, the occlusal length of each molar is near its maximum at the ontogenetic stage here represented, as the shaft of each molar is

directed strongly posterodorsad so that the occlusal surface intersects it at a highly oblique angle. In addition, the enamel columns of all cheek teeth in this specimen have undergone post-mortem separation, which has exaggerated their apparent occlusal length. Anthony felt that eruption of $M\frac{3}{3}$ in *Elasmodontomys* was unusually late in ontogeny for a "hystricomorph," indicating a tendency toward suppression. He contrasts the condition with that in *Hydrochoerus* and *Capromys,* unfortunately each representative of a group highly precocious in dental ontogeny. AMNH 17132 is here regarded as a normal stage in the ontogeny of *Elasmodontomys,* indicating that P^4 precedes M^3 in development. AMNH 55047 is only slightly more advanced than 17132, having P^4 well worn and M^3 in an early formative stage. A specimen of *Cuniculus* (MCZ 31823) represents a similar developmental stage, having $DP\frac{4}{4}$-$M\frac{2}{2}$ in use, with $M\frac{2}{2}$ newly erupted and little worn, and tiny (each less than 2 mm in diameter), superficial crypts for $M\frac{3}{3}$ present behind $M\frac{2}{2}$. No doubt this individual would have attained the full adult dentition, had it survived.[3] Definite evidence on tooth sequence in the upper dentition of *Elasmodontomys* is lacking only for the relation between M^2 and P^4. With only this point unsupported by specimens, the sequence may be given as DP^4, M^1, M^2, P^4, M^3.

The peculiar spatial relationships among the developing upper incisor, DP^4, and P^4 require special attention. In the type specimen of *"Heptaxodon bidens"* (AMNH 17101) the incisive alveoli, partially filled with matrix, terminate directly above DP^4. In specimens of *Elasmodontomys* with P^4 in use, the growing tip of the incisor intrudes between the shafts of P^4 and M^1. The shafts of the molars lie parallel to one another and are directed posterodorsad from the occlusal surface, whereas the shaft of P^4 extends anterodorsad from the occlusal surface. In old individuals (e.g. AMNH 17129) the alveolus of P^4 comes to lie shallowly under the surface of the rostrum, below the incisive alveolus. Unfortunately, growth stages between the juvenile AMNH 17101 and specimens with P^4 already functioning are not represented. These stages should be interesting developmentally as it is impossible to suppose that sufficient space could exist between the roots of DP^4 and the base of the incisor for the formation of the hypsodont P^4.

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[3] Schreuder (1933, p. 252) has also questioned Anthony's interpretation of AMNH 17132 and compared it to immature *Cuniculus.*

I would expect to find the crypt for the developing P^4 antero-dorsal to DP^4, not directly dorsal to it. X-rays of AMNH 17101 have not been altogether satisfactory owing to the super-position of images from right and left sides of the specimen, but small crypts are indeed present in the expected position just anterior to the infraorbital foramen and adjacent to the premaxillary suture. No suggestion of a cavity is present im-mediately dorsal to the base of DP^4.

LOWER DENTITION OF *Amblyrhiza*

Evidence on sequence of eruption in *Amblyrhiza* is limited to a single fragmentary left mandibular ramus in matrix (AMNH 55036). The cheek teeth are represented by vestiges of DP_4, a fully-formed but unerupted P_4, and fragmentary M_1 and M_2. P_4 extends proximally at least to the ventral mar-gin (external curve) of the incisive alveolus, a minimum length of 21 mm. The distal extremity of the tooth has been broken off level with the alveolar border, but clearly very near its tip. The three separate enamel columns are of reduced size on their broken ends, and the middle column is subdivided, with a circu-lar island at the labial extremity of its broken end — both fea-tures indicative of a fresh, unworn tooth. Immediately anterior to the alveolus of P_4 is a small, matrix-filled circular excavation about 3.4 mm in diameter, and immediately posterolingual is a shallow elongate one about 3.3 mm in anteroposterior diameter, and 1.8 mm in transverse diameter. These are undoubtedly the alveolar sockets for the roots of a deeply worn DP_4, which may have been lost after death or shed shortly prior to death. A specimen of *Chinchilla* (MCZ 7276) has a shallow pit anterior to and confluent with the alveolus of P_4 on either side of the mandible. A specimen of *Cuniculus* (MCZ 31752) has DP_4 in use on both sides, but in a very advanced state of wear, with much basal resorption. Right DP_4 is kept in place mainly by its anterior root, the posterior ones having been largely re-sorbed. The distal tip of P_4 extends above the alveolar border beneath the deeply worn DP_4. In another specimen of *Cunic-ulus* (MCZ 32078) P_4 is in use, but immediately anterior to it on either side is a shallow, transversely elongate depression which on the left side retains a small peg of DP_4. These speci-mens are, respectively, slightly younger than and slightly older than the jaw of *Amblyrhiza* in relative age.

The molars in AMNH 55036 are highly fragmentary. The remnant of M_1 does extend high above its alveolar border, and must have been functional. M_2 is broken away at the alveolar border, but its base is fully exposed (though broken) revealing that enamel growth was complete. The preserved portion of the tooth is 38.8 mm long and extends to the ventral border of the jaw. M_2 must have erupted, as indicated by its advanced development and unconstricted alveolar border. Its developmental stage lies between that of AMNH 55037 (Fig. 1D) and AMNH 55041 in *Elasmodontomys*. It is probable that the sequence of eruption was DP_4, M_1, M_2, P_4, and M_3 in *Amblyrhiza*, just as in *Elasmodontomys*.

As in *Elasmodontomys*, the shafts of the molars are directed posteroventrad, diverging proximally from the more nearly ventrally directed shaft of P_4. In older jaws of *Amblyrhiza*, the incisive alveolus extends well beyond the posterior margin of M_3.

UPPER DENTITION OF *Amblyrhiza*

The only specimen significant for the ontogeny of the upper dentition is an isolated right DP^4, AMNH 55035 (Fig. 2). The tooth is regarded as deciduous on the basis of its small size (maximum length 19.8 mm), completed enamel deposition, and anteroposteriorly elongate occlusal surface composed of five units rather than four (upper) or three (lower) as in $P\frac{4}{4}$. It is identified as DP^4 rather than DP_4 on the basis of the curvature of its shaft.

At the wear stage represented, the occlusal surface is characterized by five flattened ellipses of enamel. The first three are distinct from one another and from the fourth, but the fourth is broadly confluent with the fifth, a subcircular loop set off from the fourth only by shallow lingual and labial reëntrants. The fourth and fifth columns would have merged with much less than one millimeter of additional wear. The labial reëntrants separating columns are all quite shallow, extending proximally a maximum of 2.5 mm in the first, and decreasing successively to almost nothing in the fourth. The lingual reëntrants display a more radical decrease posteriorward in proximal extent, from 11.6 mm in the first, to 5.9 in the second, to 0.6 in the third, and practically nothing in the fourth. The tooth must have belonged to a very young animal, as its occlusal surface had
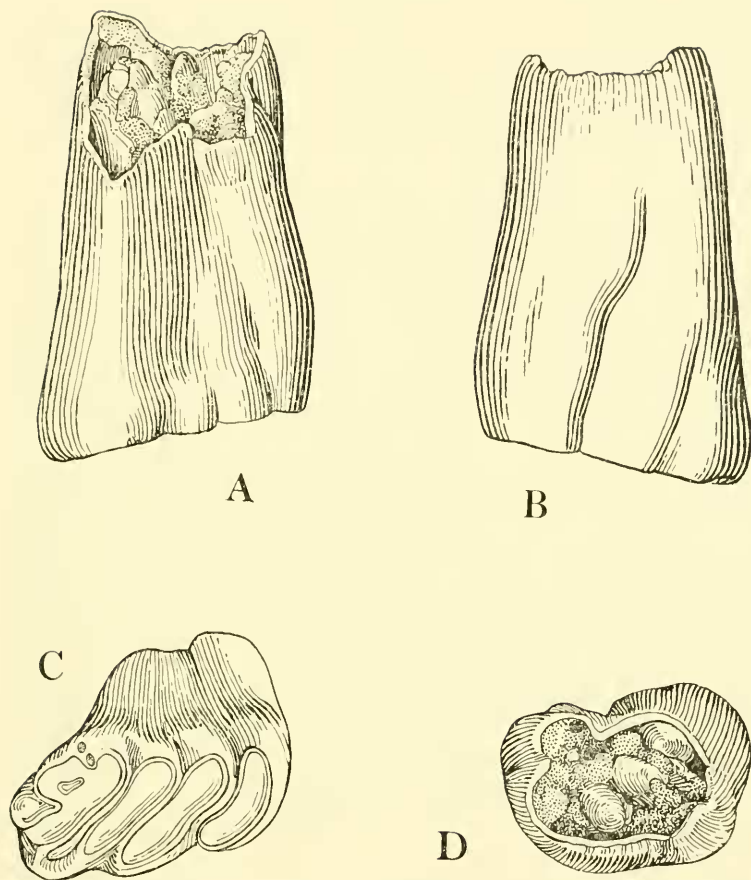
FIGURE 2. Isolated right DP^4 of *Amblyrhiza inundata* (AMNH 55035) in labial (*A*), lingual (*B*), occlusal (*C*), and proximal (*D*) aspects. Anterior is to the right in (*A*) and (*C*), to the left in (*B*) and (*D*). × 3.

yet to attain its greatest area. Breakage at the base makes it impossible to determine the status of root formation.

It may be noted here in passing that the relationship of the upper incisor to the cheek tooth row in *Amblyrhiza* is grossly different from that described above in *Elasmodontomys*. As Schreuder (1933, p. 243) has pointed out, the rostrum of *Amblyrhiza* is greatly elongated, with the upper incisor terminating far in advance of P^4, not between P^4 and M^1. I do not

feel, however, that the similarity between *Amblyrhiza* and *Chinchilla* in this feature is indicative of relationship, for *Elasmodontomys* and *Lagostomus* have short rostra with the base of the incisive alveolus overlapping and closely approaching P^4, respectively.

SUMMARY OF DENTAL ONTOGENY

"*Heptaxodon*" represents a protracted early stage in the ontogeny of *Elasmodontomys*, in which the $DP\frac{4}{4}$ constitute the sole or at least dominant functional elements in the cheek tooth series. The elongate occlusal surface with increased number of laminae in the $DP\frac{4}{4}$ presumably is correlated with this long period of use. The sequence of eruption, growth cessation, and root formation in *Elasmodontomys*, and in *Amblyrhiza* as far as the meager data show, is $DP\frac{4}{4}$, $M\frac{1}{1}$, $M\frac{2}{2}$, $P\frac{4}{4}$, $M\frac{3}{3}$.

The growing tip of the lower incisor extends progressively farther posteriorly with increasing age in *Elasmodontomys*. The condition in *Amblyrhiza* is unknown. The growing tip of the upper incisor in *Elasmodontomys* lies directly dorsal to DP^4, leaving insufficient space for the development of P^4 in that position. P^4 develops anterodorsal to the roots of DP^4 and anteroventral to the proximal end of the upper incisor. The growing tip of the upper incisor in *Amblyrhiza* lies in the greatly lengthened rostrum, far anterior to the cheek teeth. With the possible exception of the anteriorly displaced P^4 locus, every feature in the dental ontogeny of *Elasmodontomys* has been observed in other (non-heptaxodontid) caviomorphs as well.

DISCUSSION

The West Indian genera *Heptaxodon*, *Elasmodontomys*, *Amblyrhiza*, *Clidomys*, *Speoxenus*, *Spirodontomys*, and (when it has been considered) *Quemisia*, have been associated in a single subfamily. *Quemisia* will be discussed elsewhere. "*Heptaxodon*" is based on juvenile specimens of *Elasmodontomys*, and is a junior synonym of the latter. I am as yet unprepared to make pronouncements on the poorly known Jamaican forms, *Clidomys*, *Speoxenus*, and *Spirodontomys*, and thus by default prefer to leave them, at least temporarily, in association with the present group. There is little positive evidence to support the association, but neither is there justification for placing

them elsewhere in the present state of our knowledge. *Elasmodontomys* and *Amblyrhiza* assuredly are closely related, and fully warrant association at the subfamilial level. This subfamily is best regarded as a member of the family Dinomyidae, in an arrangement similar to that proposed by Schaub (*in* Stehlin and Schaub, 1951, p. 370), or possibly as a member of a family very close to the Dinomyidae (Wood, 1955, p. 182).

FAMILY-GROUP NOMENCLATURE

Anthony (1917, p. 186) proposed three monotypic subfamilies of Chinchillidae, the Amblyrhizinae, Elasmodontomyinae, and Heptaxodontinae, on successive lines of text in that order. Simpson (1945, p. 96) synonymized the three. Although Simpson neglected to mention Amblyrhizinae explicitly, his intention is clear in that he included *Amblyrhiza* in the single resultant subfamily, for which he selected the name Heptaxodontinae, a choice undoubtedly dictated by his utilization of the name Heptaxodontidae, first considered as a full family by Miller and Gidley (1918, p. 447). If subfamilial names are regarded as not influencing priority among full familial names, then Heptaxodontidae is the only valid choice. However, under the present International Code of Zoological Nomenclature (1961, Art. 23), all family-group names are regarded as coordinate for purposes of priority. In the present case, this controversial rule would have made possible the selection of a more satisfactory family name, either Amblyrhizidae or Elasmodontomyidae, both names based on older, better known genera, and as subfamilies both having line priority over the name Heptaxodontinae. Even so, Simpson, in the capacity of first reviser (International Code, 1961, Art. 24), has determined the relative priority among these simultaneously published names by selecting Heptaxodontinae as the senior synonym, and Amblyrhizinae and Elasmodontomyinae as the junior synonyms. Thus, Heptaxodontidae remains the valid name whichever system of priority is invoked. This situation is, unfortunately, not altered by the fact that *Heptaxodon bidens* Anthony 1917 is a junior synonym of *Elasmodontomys obliquus* Anthony 1916. The International Code (1961, Art. 40) states explicitly, ''when . . . a nominal type-genus is rejected as a junior synonym, a family-group name based on it is not to be changed . . .'' Thus, although there has been heated debate and strenuous disagreement on this subject, the rules are clear and ought to be followed.

The family-group name Heptaxodontinae remains available, and is not to be replaced by the name Amblyrhizinae Anthony 1917 as Schaub (*in* Stehlin and Schaub, 1951, pp. 96, 370; and 1958, p. 736) has proposed.

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